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MORPHOMETRICS AND DISTINCTNESS OF THE HEDGEHOG GENERA (INSECTIVORA: ERINACEIDAE)

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Abstract.—Five genera (*Erinaceus, Atelerix, Hemiechinus, Paraechinus, Aethechinus*) have been described in the hedgehog subfamily Erinaceinae. Using non-mensural characters, previous authors have recognized from one to five of these genera as valid. Population samples of the five named genera were compared using multivariate statistics on selected cranial measurements. Results of the statistical analyses, coupled with non-mensural characters, distribution, ecology, and fossil history, indicate that all five genera are distinct and all should be recognized.

The subfamily Erinaceinae includes five nominal genera: *Erinaceus* Linnaeus, 1758, *Atelerix* Pomel, 1848, *Hemiechinus* Fitzinger, 1866, *Paraechinus* Troussart, 1879, and *Aethechinus* Thomas, 1918. The status of these names ranges from the recognition of a single genus (*Erinaceus,* Dobson 1882), three genera (*Erinaceus, Hemiechinus,* and *Paraechinus*—see Corbet 1974, 1978; Honacki, Kinman, and Koeppl 1982), four genera (*Erinaceus, Hemiechinus, Paraechinus,* and *Atelerix*—see Dorst and Dandelot 1969), to all five as valid genera (Thomas 1918; Cabrera 1925; Allen 1939; Simpson 1945). A recent classification (Nowak and Paradiso 1983), although recognizing three genera (*Erinaceus, Hemiechinus,* and *Paraechinus*), subdivides *Erinaceus* into subgenera as: genus *Erinaceus,* with subgenera *Erinaceus* (one species) and *Atelerix* (four species, including two attributable to *Aethechinus.*

All categories above the species level include groups that are genetically and morphologically discontinuous between one another. Those taxa cannot be satisfactorily defined in absolute terms because of the possibility of the absence of a marked discontinuity between taxa of the same rank. However, a genus is generally regarded as containing one or more species phenetically separable from other genera by a decided gap between species clusters. For practical reasons, the more species in a species-group the smaller the gap needed to recognize it as a separate genus, and the smaller the number of species, the larger the gap needed to recognize it (Mayr 1969). The function of the genus is to group monophyletic (related) species and facilitate information retrieval.

Mayr (1969) gave the following criteria for delimiting and ranking taxa: (1) distinctness (size of gap)—measured in terms of phenetic distance and the biological significance of the difference; (2) evolutionary role (uniqueness of adaptive zone)—analyzed by its ecological significance and evolutionary history; (3) degree of difference—phenetically, the distance between means of two groups of species; (4) size of taxon—number of species; and (5) equivalence of ranking in related taxa.

Various combinations of characters could be used to construct a key to differentiate each of the five genera or to recognize four, three, two, or only one genus.

Because previous generic distinctions were based on non-mensural characters, we decided to compare samples of the named genera by using multivariate statistical analyses on selected cranial measurements to determine if another method would satisfactorily differentiate the genera.

In the following analyses we determine the degree of difference between groups, the type of scatter of a cluster, and whether or not there is equivalence of ranking in related taxa. The following questions were then asked and answered using results from the statistical analyses:

1) Are species clusters evident?
2) Are there gaps between the species clusters?
3) Are the species clusters of uniform density?
4) Are the species clusters large and heterogeneous?
5) Do the individual clusters include only specimens considered to be a part of the same genus (sensu stricto)?

It is also possible that a combination of mensural and non-mensural characters would better define the genera. Therefore, a sixth question was also asked:

6) Are species clusters (genera) better defined using results from statistical analyses as well as previously used non-mensural characters?

Materials and methods.—To assess the degree of difference (distinctness) of these five genera, specimens from several localities within the range of each genus were selected to include as many of their taxa as were available. Nine cranial measurements were taken and subjected to the NT-SYS multivariate statistical programs (Rohlf, Kishpaugh, and Kirk 1972) and the BMD computer programs (Dixon 1973). Character means of each sample were used when the sample size was greater than two. The standardized means or individual specimen measurements were used to compute matrices of average distance and correlation coefficients among the samples. The unweighted pair-group method using arithmetic averages (UPGMA) was used in the cluster analysis and presented as a phenogram. Non-metric multidimensional scaling (MDSCALE; Kruskal 1964a, b), were also provided by the NT-SYS programs. The BMD07M stepwise discriminant function analysis provided overall discrimination among the groups using the raw data from all individual specimens.

Specimens used in the analyses.—Species names are those recognized by Honacki *et al.* 1982. Subspecies names are included for those samples which have been named, by geographic area, in various publications. These are followed by country localities and sample size. Sample numbers used in Figs. 1 and 2 are indicated in parentheses.

Erinaceus europaeus europaeus—Germany, 10 (1); *E. e. hispanicus*—Spain, 3 (2); *E. concolor*—Turkey, 3 (3); *Paraechinus aethiopicus*—Morocco, 10 (4); Niger, 2 (6 and 7); Mauritania, 1 (5); *P. a. dorsalis*—Egypt, 4 (8); *P. a. deserti*—Egypt, 1 (11); *P. micropus*—W. Pakistan, 1 (9); *P. hypomelas*—Iran, 1 (10); *Aethechinus algirus*—Morocco, 11 (12); *A. frontalis*—South Africa, 17 and Namibia, 2 (13); *Hemiechinus auritus libycus*—Egypt, 12 (14); *H. a. aegyptius*—Egypt, 9 (15); *H. a. auritus*—Iran, 2 (16 and 17); *Atelerix albiventris albiventris*—Senegal, 22 (21); *A. a. spiculus*—Nigeria, 18 (19); *A. albiventris*—Ghana, 6 (20); Bourkina Fasso (Upper Volta), 10 (18).

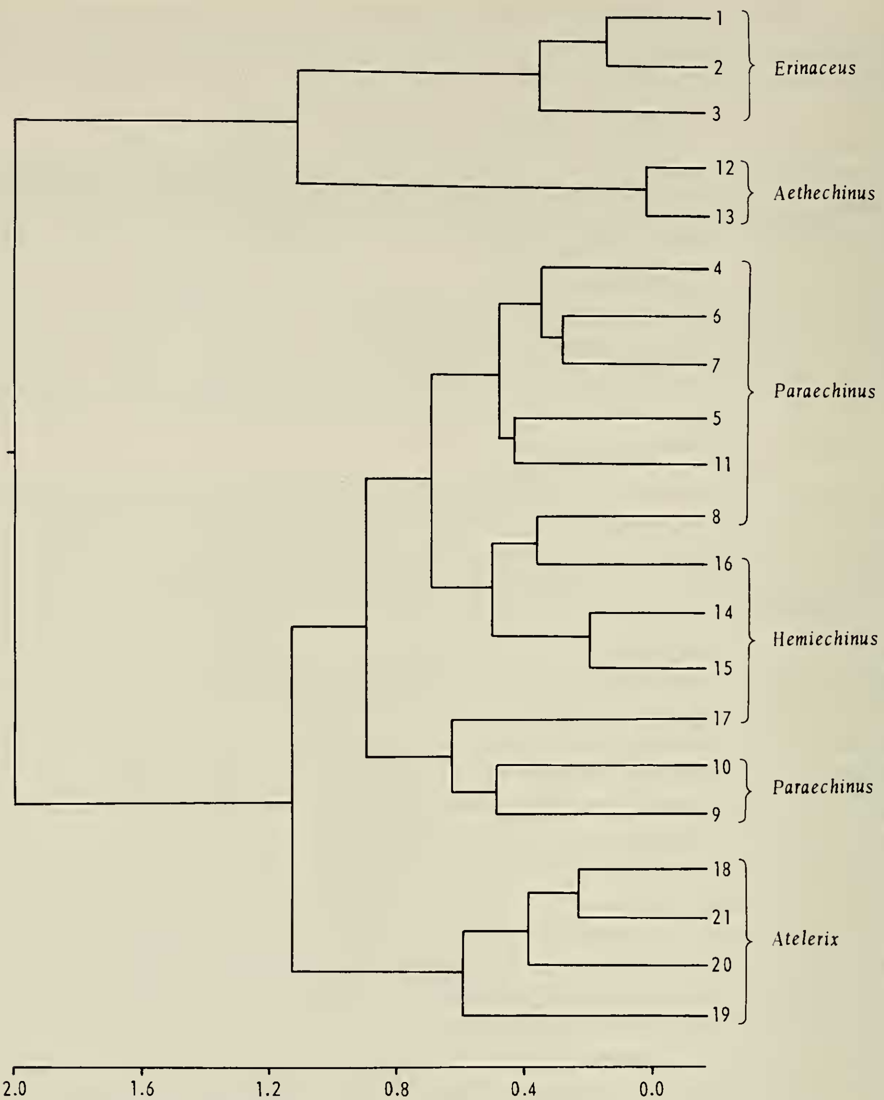

Fig. 1. Phenogram based on distance matrix of NT-SYS analysis of five genera of hedgehogs. Numbers refer to taxa and localities listed in the text. The cophenetic correlation is 0.898.

Results.—Some of the most common characters used by Anderson (1895), Miller (1912), Thomas (1918), Allen (1922), Cabrera (1925), and Corbet (1974, 1978) to compare or contrast the five genera are shown in Table 1. Morphological comparisons by Corbet (1974, 1978) led him to conclude that *Erinaceus, Atelerix,* and *Aethechinus* were congeneric (*Erinaceus*). Thus construed, *Erinaceus* incorporates all of the characters listed in Table 1 for *Erinaceus, Atelerix,* and *Aethechinus.* The remaining characters in Table 1 characterize *Hemiechinus* and *Paraechinus.*

Erinaceus, as defined by Corbet (1974, 1978), differs from both *Hemiechinus* and *Paraechinus* only by having a small postglenoid process. In addition, it differs

Table 1.—Morphological characters used to differentiate the five genera of hedgehogs.

	Erinaceus	*Atelerix*	*Aethechinus*	*Hemiechinus*	*Paraechinus*
I3 and C—no. of roots	one	two	two	two	two
P3—size	normal	reduced or absent	normal	normal	reduced
Postglenoid process vs. mastoid process	smaller	smaller	smaller	same	larger
Pterygoids and bullae size	normal	normal	normal	normal	large
Hallux	normal	generally absent	normal	normal	reduced
Posterior palatal shelf	narrow	broad	broad	narrow	narrow
Spine-part on crown	present	present	present	absent	present
Ears	small	small	small	large	large

from *Hemiechinus* by having a median spine-part on the crown of the head and from *Paraechinus* by having normal-sized pterygoids and bullae. *Hemiechinus* differs from the other two in lacking a median spine-part on the crown. It also differs from *Paraechinus* by having normal-sized pterygoids and bullae. *Paraechinus* is distinguishable from the other two genera by its inflated pterygoids and bullae.

Results of the UPGMA clustering analysis of specimens are shown as a phenogram in Fig. 1, which reveals two large and distinct clusters. *Erinaceus* and *Aethechinus* are clustered together and separated from the other three genera. Population samples of the taxa in *Erinaceus* and *Aethechinus,* as a part of the same large cluster, form distinct clusters of their own that show quite distinctive morphometric (cranial measurement) or phenetic distance between them. In the second or bottom cluster, *Atelerix* is distinct from both *Paraechinus* and *Hemiechinus.*

Figure 2, showing the MDSCALE projection, gives a better representation of the phenetic distance separating the five genera. The minimum spanning tree (Prim 1957) connects those samples closest in phenetic distance, yet shows the distances between the taxa compared. In this analysis, *Erinaceus, Aethechinus,* and *Atelerix* separate into distinct groups. The African samples of *Paraechinus* (numbers 4, 5, 6, 7, 8, 11) are also linked and clustered. The two samples of *Paraechinus* from Asia (9, 10) are linked but separated from the African samples by a specimen of *Hemiechinus* (17). The other three samples of *Hemiechinus* are linked.

A discriminant function analysis (Fig. 3) provided additional information for evaluating the morphometric differences between the five genera. The discriminant analysis shows that the degree of difference, as reflected by the distances between group means, is highly significant. The probability that all samples are allocated correctly to a particular group is $P \geq 0.90$. The probability for most is $P \geq 0.95$. The character vectors included in the figure (Power and Tamsitt 1973) show the cranial measurements and their relative contribution in the separation of the five clusters.

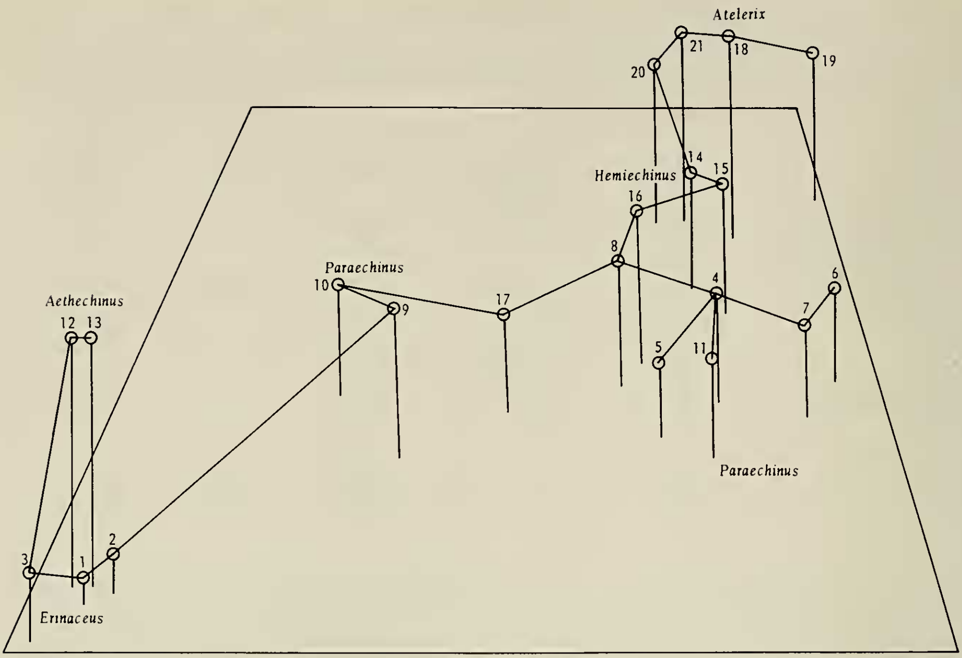

Fig. 2. Three-dimensional projection of MDSCALE analysis with minimum spanning tree for samples of hedgehog genera. For sample numbers refer to text. Stress is 0.033.

The distance between groups (size of gap) should be inversely proportional to the number of species in each group (size of taxon) in Fig. 3. For example, *Erinaceus* is represented by the fewest species but is separated from the other genera by the largest gaps and distance between group means. *Erinaceus* also has a dense species cluster. The degree of difference among the other genera is nearly equal. The distinctness of those genera, as reflected by distance (gap) between groups, varies. *Paraechinus* and *Hemiechinus* have homogeneous clusters and are separated by a decided gap. Both are separated from the other groups by even larger gaps. *Atelerix* and *Aethechinus* are closest in gap distance but the mean distance between their clusters is significant and they are well separated from the other genera. *Atelerix* has a dense and uniform cluster while the *Aethechinus* cluster is large, probably indicating greater heterogeneity.

The NT-SYS principal components analysis based on a correlation matrix (not figured) showed that cranial-size measurements (first component) separated *Erinaceus* and *Aethechinus* from the other three genera, of which *Atelerix* has the smallest skulls. *Erinaceus* was separated from *Aethechinus* in the second component, which was influenced positively by breadth of braincase and negatively by length of palatal shelf. Although *Erinaceus* has slightly larger breadth of braincase measurements than *Aethechinus,* its length of palatal shelf measurements are much smaller (see Table 1). *Paraechinus* has the largest breadth of braincase measurements relative to skull length, reflecting the inflated bullae in members of this genus. Except for *Aethechinus, Atelerix* has the longest length of palatal shelf measurements.

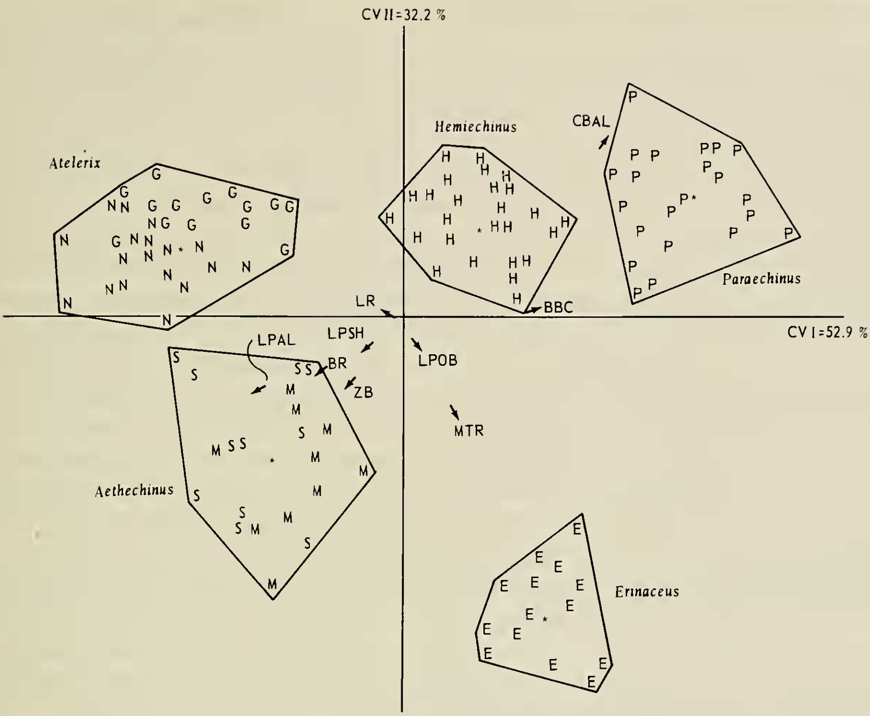

Fig. 3. Projection of the first two canonical variates in a discriminant analysis of samples of hedgehog genera. Arrows indicate vectors for the nine cranial measurements. Abbreviations are: CBAL—condylobasal length; LR—length of rostrum; MTR—alveolar length of upper molar tooth row; LPAL—length of palate; LPSH—length of palatal shelf; LPOB—least postorbital breadth; BR—breadth of rostrum; BBC—breadth of braincase; ZB—zygomatic breadth; N—Nigeria; G—Senegal; M—Morocco; S—southern Africa; CV I and CV II—canonical variates one and two; percent of cranial measurement variation accounted for by each is indicated.

Discussion and Conclusions.—The distinctiveness of each taxon based on the characters listed in Table 1 can be, as expected, subjective. The number of species recognized in each genus is also inconsistent among authors. *Erinaceus* is generally regarded as having one polytypic species, but Corbet and Hill (1980) recognized three species; *Paraechinus* contains three or four species; *Aethechinus* includes two or three species; *Hemiechinus* contains two or three species; and *Atelerix* contains several described taxa that need further study.

Butler (1978) summarized the distribution and fossil history of the five genera. He reports that *Erinaceus* is known from the Miocene to Recent in Europe, and Pleistocene to Recent in Asia in deciduous and Mediterranean woodland vegetation zones. *Atelerix* is known only from the Recent in Africa where it occurs throughout the savanna vegetation zones. *Hemiechinus* is known only from the Recent in southern Asia and northeastern Africa in semi-arid steppe or savanna regions. *Paraechinus* is known only from the Recent in southern Asia and northern Africa in desert regions. *Aethechinus* is recognized from the Recent in north and south African temperate to dry savanna habitats. These time and geographic ranges give an indication of evolutionary role, distribution, and ecological differences.

In Africa, four genera are geographically and ecologically separated. *Hemiechinus* is in the northeastern part where its range slightly overlaps that of *Aethechinus* in Libya. *Paraechinus* occurs in all of the North African deserts and slightly overlaps *Aethechinus* in Morocco and Algeria. *Atelerix* is found south of the Sahara desert in the savanna zones and does not co-occur with any other genus in the north. *Aethechinus* occurs again in southern Africa and may slightly overlap *Atelerix* in the northern part of its (*Aethechinus*) range.

Erinaceus is the only genus in Europe except for introduced *Aethechinus* which persists as localized populations in southern Spain and France. Three genera occur in Asia, with *Erinaceus* occupying the northernmost areas in the woodland steppe regions. It slightly overlaps *Hemiechinus* in some parts of its range but does not occupy the semi-arid steppe areas that *Hemiechinus* prefers. The desert-inhabiting genus *Paraechinus* slightly overlaps the range of *Hemiechinus* in some areas.

The five genera all have unique adaptive zones. Those that share similar ecologies are geographically separated. Different habitats and different distributions plus evidence from the fossil record (Butler 1978) indicate that these five also had different evolutionary histories. The differences in use of the environment are responsible for the width and distinctness of the gaps between the genera.

The six questions posed in the introduction can all be answered. Species clusters are evident; there are gaps between the clusters; four clusters are dense and uniform, the other is large and heterogeneous; each cluster includes only specimens considered to be a part of the same genus; and the species clusters are better defined using a combination of mensural and non-mensural characters.

Paraechinus and *Hemiechinus* are not clearly separated by the mensural data in Figs. 1 and 2. However, using non-mensural characters (Table 1), these distinctive genera are readily separable as was shown by Corbet (1974). This is supported by the data in Fig. 3 which show a decided gap and distance between group means. Using the results of these statistical analyses and the non-mensural characters from Table 1, five genera of hedgehogs are indicated. Morphological analyses also show that *Erinaceus* and *Aethechinus* are more closely related to each other and form a unit apart from the other three genera. If subgenera within *Erinaceus* (Nowak and Paradiso 1983) were justified, then they should be *Erinaceus* and *Aethechinus,* not *Erinaceus* and *Atelerix.* Nowak and Paradiso (1983) included species of *Aethechinus* with *Atelerix.* Morphologically, *Aethechinus* and *Atelerix* are not closely related. Their fossil records (Butler 1978) and geographic distributions suggest to us that European and Asian *Erinaceus* could have given rise to *Aethechinus,* which is now represented by separate species in northern and southern Africa.

Generic classifications using qualitative characters that recognize fewer than five genera need modification. Equivalence of ranking in related taxa, when applying unweighted non-mensural characters, can only result in the recognition of one or five genera. The results from the morphometric analyses of cranial measurements support the recognition of five genera (*Erinaceus, Aethechinus, Paraechinus, Hemiechinus,* and *Atelerix*) as given by Thomas (1918), Cabrera (1925), Allen (1939), and Simpson (1945). Recognition of five genera of hedgehogs also groups closely related species and avoids unnecessarily complicated arrangements resulting from using any other taxonomic grouping. Such an interpretation is possible using non-mensural morphological characters coupled with results of the statistical analyses.

Erinaceus: Relatively large animals with long and broad skulls; CBAL usually greater than 55 mm; I3 and C single rooted; P3 normal in size; postglenoid process smaller than mastoid process; pterygoids and bullae normal (not inflated); palatal shelf narrow; hallux well developed; a median spine-part present on crown of head; ears small, not projecting above head-spines.

Hemiechinus: Medium to large animals with medium to large skulls; CBAL ranges from 45 to 55 mm; I3 and C double rooted; P3 normal; postglenoid process same size as mastoid process; pterygoids and bullae normal; palatal shelf narrow; hallux well developed; median spine-part on crown of head absent; ears large, projecting above head-spines.

Aethechinus: Large animals with large skulls; CBAL ranges from 45 to 60 mm; I3 and C double rooted; P3 normal; postglenoid process smaller than mastoid process; pterygoids and bullae normal (not inflated); hallux well developed; palatal shelf broad; median spine-part on crown present; ears small.

Paraechinus: Medium animals with medium length but broad skulls; CBAL ranges from 40 to over 50 mm; I3 and C double rooted; P3 reduced in size; postglenoid process larger than mastoid process; pterygoids and bullae markedly inflated; hallux reduced; palatal shelf narrow; median spine-part on crown present; ears large, projecting well above head-spines.

Atelerix: Small animals with small skulls; CBAL usually less than 45 mm; I3 and C double rooted; P3 reduced or absent; postglenoid process smaller than mastoid process; pterygoids and bullae normal; palatal shelf broad; hallux usually absent, but if present then greatly reduced in size; median spine-part on crown present; ears small.

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